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Original article

On the association of giant short-faced bear (*Arctodus simus*) and brown bear (*Ursus arctos*) in late Pleistocene North America[☆]

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ABSTRACT

Climate change and human impacts are often implicated in Quaternary megafaunal extinctions. The discovery of associated remains of extinct giant short-faced bears (*Arctodus simus*) and invading brown bears (*Ursus arctos*) raises the possibility of competition as another potential factor. We describe fossil remains of both genera from Pellucidar Cave, Vancouver Island, Canada. Analyses of ancient mitochondrial DNA support the identifications of post-cranial brown bear specimens and assign these bears to Clade 4. Our results are consistent with the migration of brown bears from Eastern Beringia to the contiguous United States before the Last Glacial Maximum (LGM) and to Vancouver Island as environmental conditions became favorable after the LGM. Radiocarbon age estimates on these specimens indicate the presence of giant short-faced bears approximately 13.5 thousand calibrated years before present (cal. ka BP; uncalibrated $11,775 \pm 30$, $11,720 \pm 50$, and $11,615 \pm 30$ BP) and of brown bears immediately preceding (~14.5 cal. ka BP; $12,440 \pm 35$, $12,425 \pm 30$ BP) and following this time (~13 cal. ka BP; uncal. $11,100 \pm 30$ BP), suggesting niche partitioning to reduce competition among these species. We suggest that shifts in food availability or quality due to post-glacial vegetation and faunal changes were probably of primary importance in the arrival and the disappearance of giant short-faced bears on Vancouver Island. This study focuses on a key time period and geographic location that is useful in understanding Pleistocene extinctions in North America.

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1. Introduction

During the Pleistocene, the giant short-faced bear *Arctodus simus* Cope, 1879, was found across North America, both in the continental United States (U.S.A.) and in Beringia (Kurtén and Anderson, 1980), the isthmus that was exposed between Alaska and Asia during glacial periods. As the Pleistocene ended, giant short-faced bears became extinct, with latest known fossil specimens dated to approximately 10.9–10.7 ka BP, i.e., ~12.7 thousand calibrated calendar years before present (cal. ka BP), from Kansas, Texas, and Utah (Madsen, 2000; Schubert, 2010). These large bears were one of 17 late Pleistocene genera to go extinct in North America after 12 ka BP (Grayson, 2015) as climate changed and human presence increased so that these factors are often implicated in the extinctions (Barnosky et al., 2004; Grayson, 2007, 2015; Meltzer, 2015). Here we focus on an additional

potential factor: the role of competition with brown bears *Ursus arctos* Linnaeus, 1758, in the extinction of giant short-faced bears.

In what is now the continental U.S.A., giant short-faced bears may have been out-competed by invading brown bears as the latter expanded southward from Beringia (Kurtén and Anderson, 1974). Some evidence for this hypothesis comes from Eastern Beringia, where brown bears date from ~48 to ~7 ka BP with a gap in radiocarbon dates from ~34 to ~20 ka BP, and where giant short-faced bears date from ~44 to ~20 ka BP that likely marked the end of the genus in this region (Harington, 2003: pp. 381–383). Stable isotope analysis of fossil bone shows that brown bears shifted to a more carnivorous diet around 20 ka BP compared to their pre-35 ka BP predecessors, suggesting that brown bears could have competed for resources with giant short-faced bears in that region (Barnes et al., 2002).

To address the competition hypothesis, we report an association of brown bear and giant short-faced bear bones from Pellucidar Cave on Vancouver Island, British Columbia (B.C.), in southwest Canada. We present new radiocarbon age estimates to determine the temporal relationship between these species at this

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locality and examine if inter-species competition for territory may have been a factor in the local extirpation of these bears. Additionally, for information about the biogeography of brown bears to that of short-faced bears, we obtained ancient mitochondrial deoxyribonucleic acid (*aDNA*) data from three brown bear specimens and use them in an attempt to discover the origin of ancient brown bears on Vancouver Island. The two nearest extent populations of brown bears represent genetically distinct mitochondrial DNA clades. Contemporary populations from north of Vancouver Island along the B.C. coastline and from central interior B.C. carry Clade 3b (Miller et al., 2006), which is also found across continental Alaska and the Yukon. In contrast, populations to the east and south of Vancouver Island belong to mitochondrial Clade 4, as do all populations from southern Canada and the contiguous U.S.A. The ancestors of Clade 4 likely migrated south from eastern Beringia between 89 and 35 ka BP (median ~56 ka BP; Leonard et al., 2000; Barnes et al., 2002; Davison et al., 2011; Edwards et al., 2011). The last Alaskan individuals related to this group dates to ~36 ka BP (Barnes et al., 2002; Edwards et al., 2011), and a Clade 4 individual from Edmonton, Alberta, dates to ~26 ka BP (Matheus et al., 2004), indicating a biogeographic track east of the Rocky Mountain Range. The documented historic range of brown bears (Miller et al., 2006; Fig. 3a) indicates Vancouver Island is within the narrow region where the Clade 3b and Clade 4 groups nearly connect. This distribution allows us to test whether the ancestors of the Pellucidar Cave brown bears originated as Clade 3b from central and northern B.C., where giant short-faced bears are not known, or as Clade 4 from an eastern and/or southern continental source where giant short-faced bears occurred (Richards et al., 1996).

We describe some of the first ancient brown and giant short-faced bear specimens from Vancouver Island (see also Steffen and Harington, 2010; Steffen, 2016), and discuss these specimens in the contexts of possible competitive interactions, the effects of a changing environment, and implications for humans to gain insights into the causes of the extinction of the giant short-faced bear *Arctodus simus*.

2. Geologic setting

2.1. Locality

Pellucidar Cave (1:50,000 NTS map sheet 092L07) is located on northeast Vancouver Island (Fig. 1) near the north edge of the Vancouver Island Ranges physiographic unit and south of the Nahwitti Lowland (Holland, 1976; Howes, 1983). The cave comprises a series of passages in Quatsino Limestone (Nixon et al., 2006), at approximately 600 m elevation above sea level, on the eastern slopes of Nimpkish Lake. Nagorsen and Keddie (2000), Harington (2011), and Steffen (2016) provide information about the locality that includes two entrances. The Pellucidar II opening, referred to in this paper as Pellucidar Cave, is a rubble-choked entrance situated on steep terrain at the base of a steep cliff face.

2.2. Stratigraphy

Bone specimens were located on the ground surface of the inward-sloping main passage, within 60 m of the entrance to the cave, amongst angular roof-fall and limestone and exotic (primarily granitic) sub-rounded boulders and cobbles that were a former streambed. Survey, mapping and then collection resulted in the assemblage of bone specimens reported here (Fig. S1, Appendix B). Each of the brown bear specimens was found at a separate location on the passage floor and these specimens

represent at least two individuals. Giant short-faced bear specimens are the partial remains of one individual found as a concentration of bone fragments amongst fluvial deposits.

3. Material and methods

3.1. Material

Bone specimens are portions of a cranium (PC2-1a-d and PC2-7) and a partial humerus (PC2-3) of a giant short-faced bear (*Arctodus simus*; Fig. 2), as well as a partial femur (PC2-2), the distal portion of a humerus (PC2-11), and the humerus of an immature individual (PC2-13) of brown bear (*Ursus arctos*; Fig. 3).

Specimens described in this study are housed in the permanent collections of the Royal BC Museum in Victoria, B.C., Canada, and have assigned RBCM catalogue numbers as noted. A list with institutional abbreviations of comparative specimens examined in this study is provided in Appendix A. Final genetic sequences have been entered into GenBank under the accession numbers JX448567–JX448569.

3.2. Measurements

Measurements follow Merriam and Stock (1925), Kurtén (1967) and von den Driesch (1976). Additional measurements are of the entepicondylar foramen of humerus PC2-3, and the minimum length of diaphysis measured from base of the proximal articular surface to the capitulum of humerus PC2-13. Measurements of femur PC2-2 include the minimum anteriorposterior diameter of the diaphysis, minimum length from the trochanteric fossa to the intercondyloid fossa, and minimum depth at the center of distal articular surface. Measurements of the alveoli of the maxilla fragment are also given.

3.3. Radiocarbon dating

Six radiocarbon samples were obtained from the Pellucidar Cave bear specimens (Table 1). Two samples on giant short-faced bear (PC2-1c and PC2-3) and three samples on brown bear (PC2-2, PC2-11, and PC2-13) were sent to the Keck Carbon Cycle Accelerator Mass Spectrometry (AMS) facility at the University of California, Irvine. Radiocarbon was measured on ultrafiltered (> 30 kD) collagen according to Brown et al. (1988) and Beaumont et al. (2010). Results have been corrected for isotopic fractionation according to the conventions of Stuiver and Polach (1977), and $\delta^{13}\text{C}$ values were measured on prepared graphite with AMS. A sample of dentine from the posterior labial root of the M2 of the maxilla fragment (PC2-1a) was sent to a second lab, the Oxford Radiocarbon Accelerator Unit in the Research Laboratory of Archaeology and the History of Art at Oxford, United Kingdom, where the chemical pretreatment, target preparation and AMS measurements follow Bronk Ramsey et al. (2004). Radiocarbon ages were converted to calendar ages with the IntCal13 calibration curve (Reimer et al., 2013) using the OxCal 4.2 radiocarbon calibration software (Bronk Ramsey, 2009).

3.4. Ancient DNA isolation, amplification, and sequencing

Bone samples removed from specimens of giant short-faced bear (PC2-3), and brown bear (PC2-2, PC2-11, and PC2-13) were processed using standard *aDNA* protocols, including the use of extraction and PCR negatives (Gilbert et al., 2005). Sample storage, *aDNA* extraction and polymerase chain reaction (PCR) set-up was performed in a dedicated *aDNA* facility at Penn State University

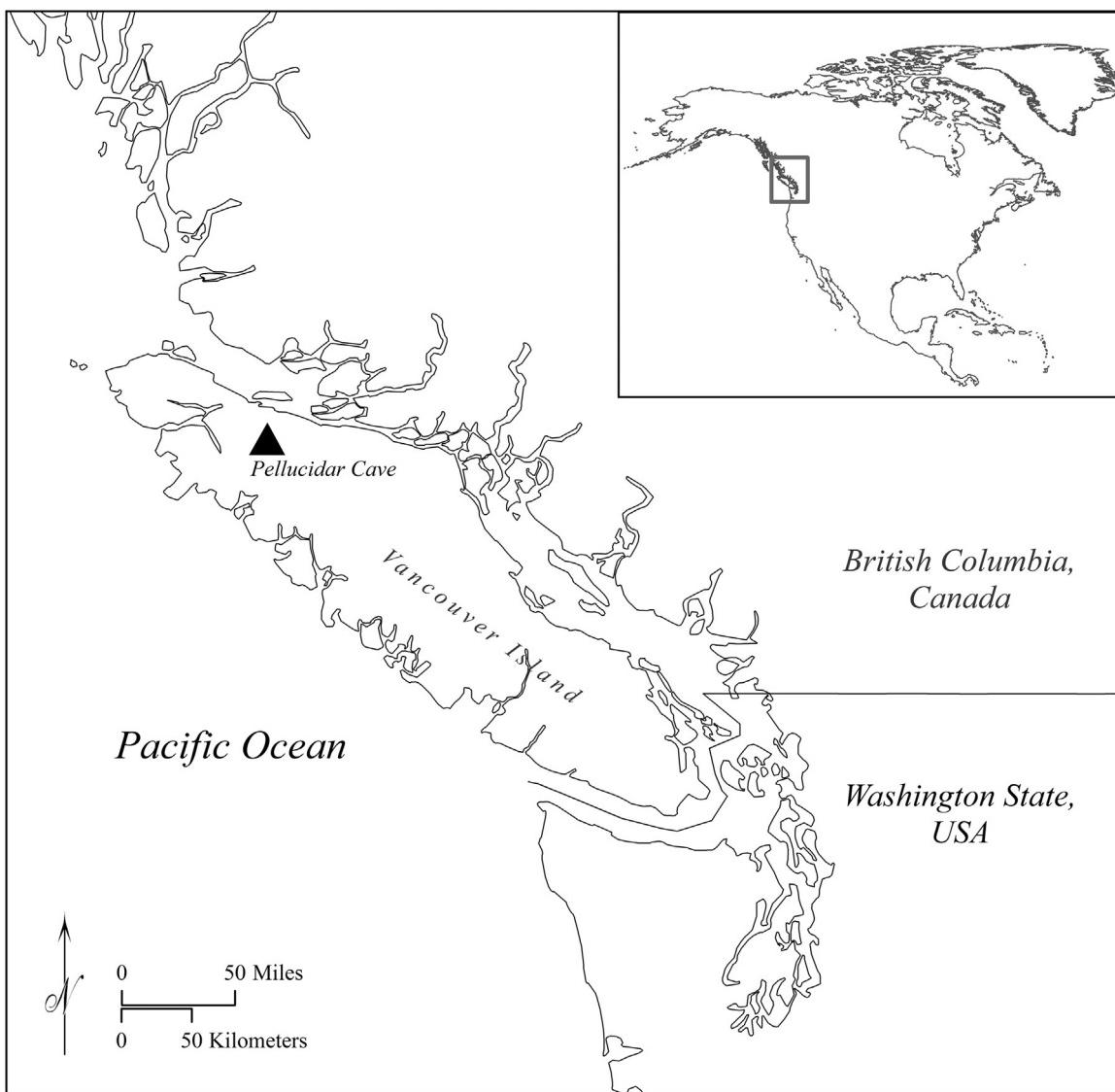


Fig. 1. Map showing the approximate location of Pellucidar Cave on Vancouver Island, British Columbia, Canada.

that is physically isolated from modern PCR products and downstream genetic work. *aDNA* was isolated from the specimens following Rohland and Hofreiter (2007). For the three brown bears, a segment of the mitochondrial control region was PCR amplified in a 25 μ L reaction comprising: 2 mg/mL rabbit serum albumin, 1X AmpliTaq Gold 360 buffer (Applied Biosystems Inc., Foster City, California), 1.25 U Amplitaq Gold360, 250 μ M each dNTP, 2.5 mM MgCl₂, 1 μ M each primer URSUSF1–136–156 (Valdiosera et al., 2007) and H16299 (Hänni et al., 1994). Cycling conditions were used as per the manufacturer's instructions with a 58 °C annealing temperature. The PCR product was cleaned using Millipore Multiscreen PCR_μ96 filter plate (Millipore, Billerica, Massachusetts) and directly sequenced using BigDye v3.1 sequencing chemistry (Applied Biosystems) and the same primers as for amplification. Sequences were purified using ethanol precipitation and resolved using an Applied Biosystems 3730xl capillary sequencer at the University Park Genomics Core Facility (Penn State University). Two short (60 bp and 135 bp) fragments internal to the longer fragment were amplified and sequenced as in Barnes et al. (2002). No mismatches were identified between overlapping fragments. The final sequences were 275 bp (PC2-2), 253 bp (PC2-13), and 295 bp (PC2-11) long. No endogenous DNA could be recovered from the

short-faced bear specimen, PC2-3, using as short as a 60 bp fragment (Hänni et al., 1994).

3.5. Genetic analysis

The NCBI BLAST program was used to genetically identify the specimens as brown bear. The sequences were aligned to other modern and ancient brown bear and polar bear *Ursus maritimus* Phipps, 1774, control region sequences available from GenBank (Table S1, Appendix B). The intraspecific relationships of the specimens were determined using BEAST v.1.8.2 (Drummond and Rambaut, 2007). The HKY+G model of nucleotide substitution was selected using ModelTest (Posada and Crandall, 1998) and a flexible coalescent prior, the Bayesian skyline plot (Drummond et al., 2005), was used with 10 groups. Mean AMS radiocarbon dates for ancient specimens were used to calibrate the clock. Three Markov Chain Monte Carlo (MCMC) chains were run for 100 million generations each, subsampling every 10,000 generations and discarding the first 10% of samples as chain burn-in. Remaining samples were combined in LogCombiner. Effective sample sizes and MCMC convergence were assessed using Tracer v1.6 (Rambaut and Drummond, 2007) and the maximum clade credibility tree (Fig. 4; Fig. S2, Appendix B) was summarized using TreeAnnotator.

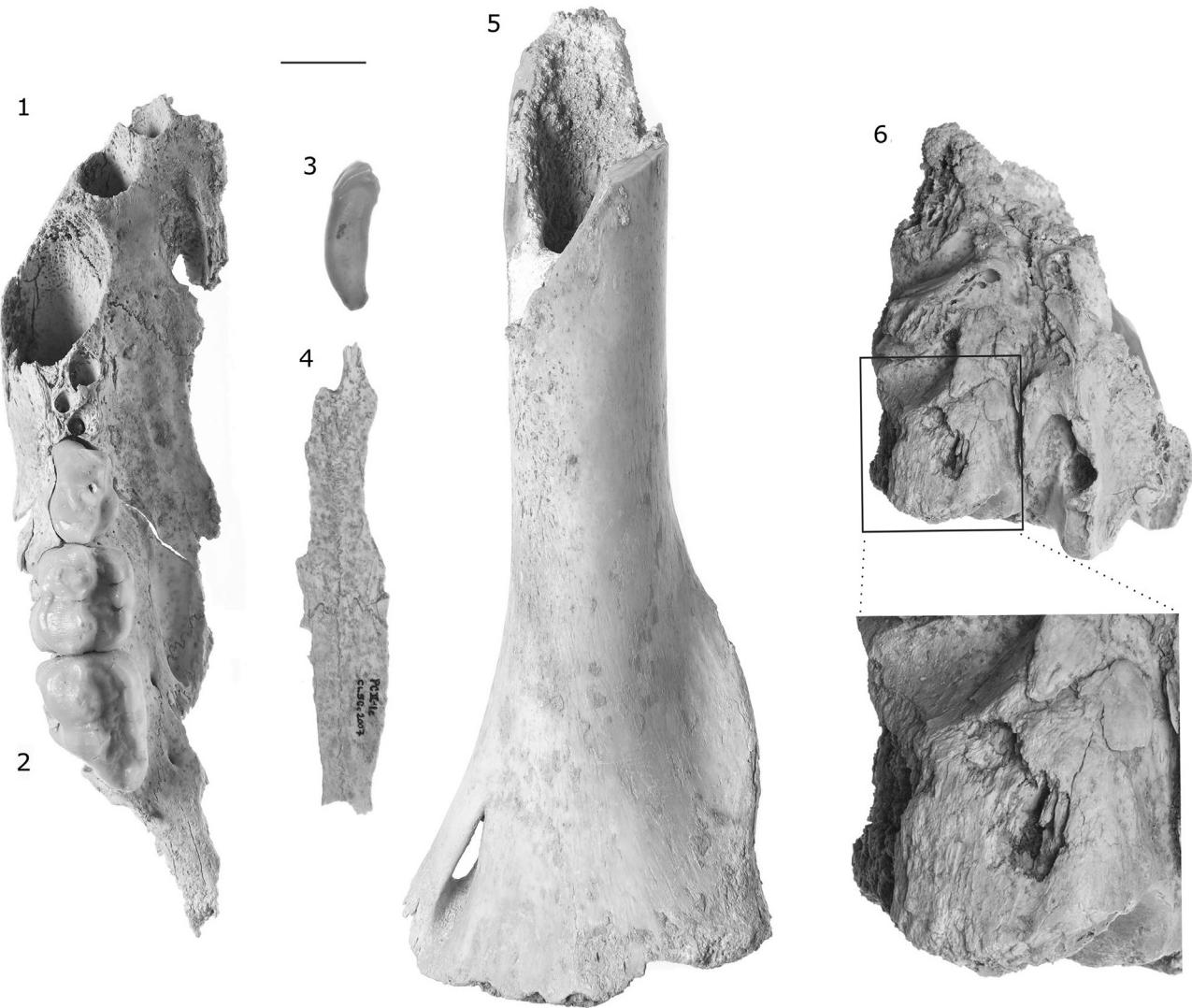


Fig. 2. *Arctodus simus* specimens from Pellucidar Cave, Vancouver Island (British Columbia, Canada). **1.** PC2-1b, portion of a right maxilla in occlusal view. **2.** PC2-1a, portion of a right maxilla with P⁴–M² and part of the palatine process in occlusal view. **3.** PC2-1d, right l¹ in lateral view. **4.** PC2-1c, central palatine bone fragment in inferior view. **5.** PC2-3, distal portion of a left humerus in anterior view. **6.** PC2-7, left skull fragment (top); the enlarged area (bottom, not to scale) shows probable bear m1 tooth puncture. Scale bar: 2 cm.

4. Results

4.1. Systematic paleontology

Bone specimens are five fragments of a cranium and one partial humerus assigned to the giant short-faced bear *Arctodus simus* (Fig. 2), and a partial femur, the distal portion of a humerus and the humerus of an immature individual assigned to the brown bear *Ursus arctos* (Fig. 3).

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Ursidae Gray, 1825

Subfamily Tremarctinae Merriam and Stock, 1925

Genus *Arctodus* Leidy, 1854

Arctodus simus (Cope, 1879)

Fig. 2

Synonymy: 1879. *Arctotherium simum* nov. sp. – Cope, p. 791; Cope, 1891, Plate XXI.

1911. *Arctotherium californicum* nov. sp. – Merriam, 1911, p. 164, figs. 1–3.

1911. *Arctotherium yukonense* nov. sp. – Lambe, 1911, p. 21, pt. 1–3.

1916. *Dinarctotherium merriami* nov. sp. – Barbour, 1916, p. 349, pt. 26, figs. 1–6.

Material: Partial cranium with most of the right maxilla in several fragments PC2-1a, b, c; palatine fragment PC2-1d; partial left humerus PC2-3.

Description: The PC2-1a (Fig. 2(2); Table 2) specimen is a right maxilla including the right upper fourth premolar to the right upper second molar (P4–M2). The teeth are well preserved. However, there is damage to the root of the M2, the posterior root of M1, the paracone and metacone, and to the enamel on the labial margin of P4. The P4 of the PC2-1a specimen shows evidence of dental caries, and is broken as to not retain a complete shearing attribute. We assign PC2-1a to *A. simus* based on the shape and size of the P4, M1, and M2, a partial shearing attribute in P4, as well as the high degree of crowding in the tooth row. The Pellucidar specimen is from a young adult according to degree of wear on the occlusal surfaces of the teeth, and is from a relatively small individual – possibly female – that compares well with *A. simus* from Potter Creek Cave, California (Kurtén, 1967).

Cranial fragments PC2-1a-d (Fig. 2(1–4); Table 2) were found together in contact at the fossil locality and are from the same *A. simus* individual. Fragment PC2-1b (Fig. 2(1)) includes an anterior

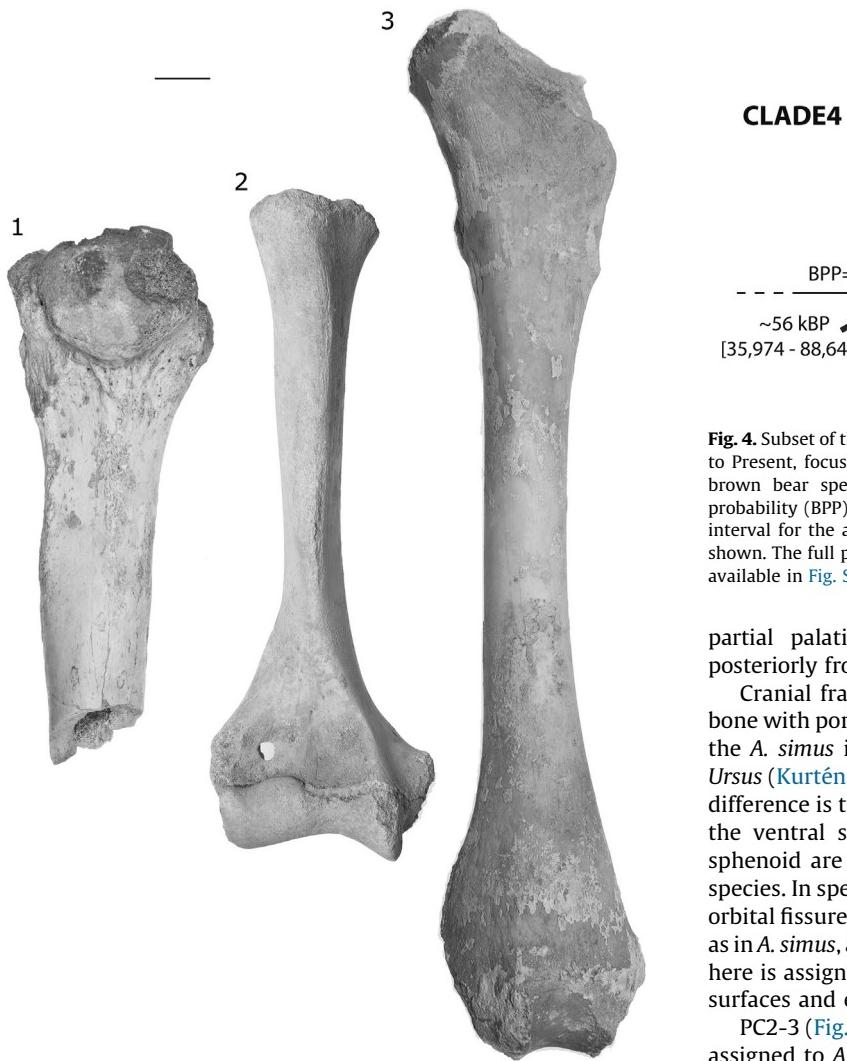


Fig. 3. *Ursus arctos* bones from Pellucidar Cave, Vancouver Island (British Columbia, Canada). **1.** PC2-11, proximal half of left humerus in caudal view. **2.** PC2-13, right humerus lacking the proximal epiphysis in anterior view. **3.** PC2-2, partial left femur in anterior view. Scale bar: 2 cm.

portion of the maxilla, part of the palatine process with anterior palatine foramen, and a portion of the premaxilla including alveoli for the relatively large upper third incisor and progressively smaller I2 and I1 that, other than damaged margins, are nearly complete. Posterior to the canine alveolus are three small premolar alveoli of which the first premolar is the largest. The maxillary-premaxillary suture is visible at the anterior margin of C1 and most of the right transverse palatine suture is preserved. According to the best-fit in the alveoli of the Pellucidar cranial fragments, specimen PC2-1d (Fig. 2(3)) is a lightly worn right I1. Specimen PC2-1c (Fig. 2(4)) is a

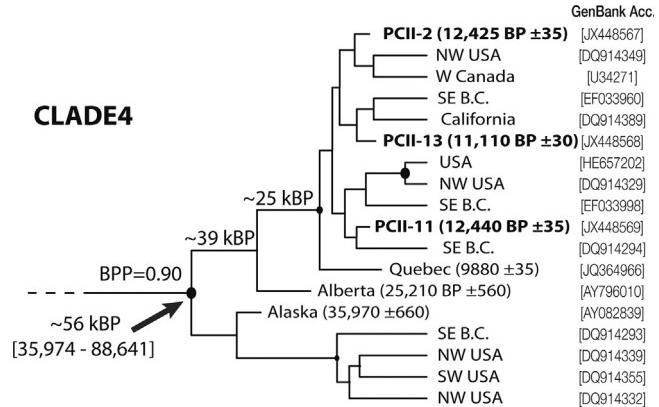


Fig. 4. Subset of the molecular phylogeny of brown and polar bears from ~56 ka BP to Present, focusing on the recovered relationships of the three Pellucidar Cave brown bear specimens. Black circles are proportional to Bayesian posterior probability (BPP) support for nodes that received $BPP \geq 0.50$. The 95% credibility interval for the age of the last common ancestor of these Clade 4 individuals is shown. The full phylogeny, including GenBank accession numbers as tip labels, is available in Fig. S2, Appendix B.

partial palatine bone with a mid-palatine suture that runs posteriorly from the partially preserved incisive foramen.

Cranial fragment PC2-7 (Fig. 2(6)) is the partial left temporal bone with portions of the adjoining parietal and sphenoid bones of the *A. simus* individual. Skull shape distinguishes *Arctodus* from *Ursus* (Kurtén, 1967; Merriam and Stock, 1925). One aspect of this difference is the relative positioning of the numerous foramina on the ventral surface of the cranium, as these openings on the sphenoid are relatively more crowded in *A. simus* than in *Ursus* species. In specimen PC2-7 the position of the optic canal, superior orbital fissure, foramen rotundum, and foramen ovale are crowded as in *A. simus*, and based on this characteristic the specimen studied here is assignable to this species. The fragment has crushed bone surfaces and edges and shows an elongate tooth impression.

PC2-3 (Fig. 2(5); Table 3) is a distal portion of a humerus that is assigned to *A. simus* based on the presence of an entepicondylar foramen and large size (Kurtén and Anderson, 1980). Measurements of the PC2-3 entepicondylar foramen and the piece of bone covering the foramen were found to differentiate the fossil specimen from those of modern black bears (Table 3). The break near midshaft, possibly made on fresh bone by a relatively strong impact, is a spiral fracture. The distal epiphysis of this bone specimen is absent and the articular surface is damaged and irregular, making it difficult to determine if the epiphysis was fused at the time of death of the animal.

Remarks: Osteological characters that differentiate the fossil remains of Tremarctine and Ursinae bears – the two bear subfamilies indigenous to North America – include an extra lateral cusp between the trigonid and talonid on the m1, and a premasseteric fossa on the mandible in the former. Although not limited to *Arctodus*, an entepicondylar foramen on the humerus along with large size can be

Table 1

Radiocarbon age estimates on bear bones from Pellucidar Cave ("PC" specimens) and from northern Vancouver Island ("SC-1" specimen). Calibrated age ranges were calculated using OxCal 4.2 (Bronk Ramsey, 2009).

Lab #	Specimen #	Material	$\delta^{13}\text{C}$	C:N atomic	^{14}C age BP	2σ cal. age ranges (BP)
UCIAMS 41052	PC2-13	<i>Ursus arctos</i> - immature humerus	-22.6	3.17	$11,110 \pm 30$	13,082–12,845
UCIAMS 41049	PC2-1c	<i>Arctodus simus</i> - palatine	-18.8	3.16	$11,615 \pm 30$	13,557–13,379
OxA 24005	PC2-1a	<i>Arctodus simus</i> - M2	-18.6	—	$11,720 \pm 50$	13,715–13,440
UCIAMS 41048	PC2-3	<i>Arctodus simus</i> - humerus	-18.7	3.22	$11,775 \pm 30$	13,725–13,477
UCIAMS 56479	SC-1	<i>Ursus americanus</i> - cranium	-21.0	3.20	$11,935 \pm 40$	13,964–13,575
UCIAMS 41050	PC2-2	<i>Ursus arctos</i> - femur	-18.1	3.19	$12,425 \pm 35$	14,836–14,211
UCIAMS 41051	PC2-11	<i>Ursus arctos</i> - humerus	-18.8	3.19	$12,440 \pm 35$	14,888–14,239

— indicates that the $\delta^{15}\text{N}$ value was not provided by the laboratory, therefore C:N atomic was not calculated.

Table 2Comparative measurements (in mm) of skull fragments PC2–1 from Pellucidar Cave with Pleistocene *Arctodus simus*.

Tooth	Measurement	<i>Arctodus simus</i> , Pellucidar Cave			<i>Arctodus simus</i> , Pleistocene		
		RBCM PC2–1a	Mean	Range (N)	SD		
I1	Greatest transverse diameter	8.26	9.0	8.8–9.2 (5)	0.1		
	Transverse diameter of alveolus	6.5					
I2	Transverse diameter of alveolus	7.8					
I3	Transverse diameter of alveolus	13.5					
C1	Transverse diameter of alveolus	30.2					
P1	Transverse diameter of alveolus	7.6					
P4–M2	Anteroposterior diameter	79.1	82.32	76.0–87.9 (11)		^a	
P4	Anteroposterior diameter	22.1	22.01	19.4–25.7 (33)		^a	
	Greatest transverse diameter	–	16.37	14.3–18.9 (32)		^a	
M1	Anteroposterior diameter	25.4	25.74	23.2–28.3 (44)		^a	
	Greatest transverse diameter (anterior width)	22.7	24.4	19.8–26.3 (44)		^a	
M2	Anteroposterior diameter	36.24	37.39	33.3–42.9 (42)		^a	
	Greatest transverse diameter (anterior width)	23	23.68	20.8–26.6 (42)		^a	

^a Measurements from Richards et al. (1996), (Appendix B); SD not available.**Table 3**Comparative measurements (in mm) of distal humerus PC2–3 from Pellucidar Cave with *Arctodus simus* and Modern *Ursus americanus*.

Measurement	PC2–3	<i>Pellucidar Cave</i>			<i>Arctodus simus</i> , Potter Creek Cave			<i>Ursus americanus</i> , Modern		
		Mean	Range (N)	SD	Mean	Range (N)	SD	Mean	Range (N)	SD
Transverse diameter of the diaphysis at midshaft	36.8	39.2	35.1–41.7 (4)	2.9	28.84	24.1–32.59 (3)	4.33			
Maximum mediolateral diameter at superior margin of entepicondylar foramen	66.0	64.8	66.1–63.5 (2)	64.8	48.4	39.5–52.9 (3)	7.7			
Minimum anterolateral diameter at superior margin of entepicondylar foramen	34.0	36.6	33.1–38.9 (4)	2.5	24.5	19.1–28 (3)	4.7			
Anterior length of slip of bone covering the entepicondylar foramen	32.5	32.6	26.5–37.6 (4)	4.6	15.9	15.4–16.6 (3)	0.61			
Width at middle of slip of bone covering the entepicondylar foramen	11.7	13.3	11–15 (4)	1.7	6.4	4.7–8.2 (3)	1.8			
Thickness at middle of the slip of bone covering entepicondylar foramen	5.3	5.7	5.1–6.2 (4)	0.5	3.9	2.9–4.5 (3)	0.9			

useful in differentiating these bears from *Ursus* (Merriam and Stock, 1925; Kurtén and Anderson, 1980). The maxillary teeth of *Arctodus* are distinguished from those of *Ursus* based on the protocone in P4 at a more anterior position than in *Ursus*, in the presence of an enamel ridge that extends between the apices of the paracone and metacone forming a shearing blade on P4, and by molars that are relatively short and broad in *Arctodus* (Merriam and Stock, 1925; Kurtén, 1967). Larger, wider, and more crowded teeth, as well as molar proportions differentiate *A. simus* from *A. pristinus* (Kurtén, 1967; Kurtén and Anderson, 1980; Emslie, 1995; Schubert et al., 2010). Because *A. pristinus* is restricted in time to no later than the middle Pleistocene (Emslie, 1995; Schubert et al., 2010), and to a geographic range in eastern North America (Kurtén, 1967) and Central Mexico (Dalquest and Mooser, 1980), we regard the *Arctodus* specimens described above as too young and too distant from the geographic range of *A. pristinus* to be assignable to that species.

Subfamily Ursinae G. Fisher, 1817

Genus *Ursus* Linnaeus, 1758*Ursus arctos* Linnaeus, 1758

(Figs. 3.1–3.3)

Synonymy: Numerous species and subspecies have been assigned to this Holarctic bear (Pasitschniak-Arts, 1993);

synonyms for this species are extensive and are not repeated here (Wilson and Reeder, 2005).

Material: The proximal half of a left humerus (PC2–11); a right humerus (PC2–13); a left femur (PC2–2).

Description: PC2–11 (Fig. 3(1); Table 4) is the proximal half of a left humerus. Features used to characterize this bone are the proximal portion of the deltoid ridge, a posterior portion of the intertuberal groove, and the teres eminence that appear prominently in this specimen as in *Ursus* (Merriam and Stock, 1925). Midshaft width and midshaft depth of the PC2–11 specimen are within the size range of adult brown bears, being both slightly larger than black bear and smaller than giant short-faced bear comparative material (Table 4). Ancient DNA analysis provides additional confirmation of the identification of this specimen as *U. arctos*. Carnivore tooth impressions are present on the shaft and humeral head.

Specimen PC2–13 (Fig. 3(2); Table 5) is the right humerus of an immature bear. The proximal epiphysis of the humerus was not fused, as the proximal surface of the shaft shows signs of erosion. Suture lines are visible on the distal epiphysis. Prominent deltoid and supinator ridges and the absence of an entepicondylar foramen are features of this specimen consistent with *Ursus* (Merriam and Stock, 1925). The size of the PC2–13 specimen was compared with modern brown and black bears that have unfused proximal and

Table 4Comparative measurements (in mm) of proximal humerus PC2–11 from Pellucidar Cave with Modern *Ursus arctos* and *U. americanus* and Pleistocene *Arctodus simus* humeri.

Measurement	<i>Ursus arctos</i> , Pellucidar Cave			<i>Ursus arctos</i> , Modern			<i>Ursus americanus</i> , Modern			<i>Arctodus simus</i> , Pleistocene		
	PC2–11	Mean	Range (N)	SD	Mean	Range (N)	SD	Mean	Range (N)	SD		
Greatest length of complete specimens	–	352.4	287–450 (14)	45.9	286.8	247–324 (18)	24.4	484.4	436–633 ^a (13)	–		
Transverse diameter at the middle of the diaphysis	33.8	35.4	25.3–51.3 (17)	7.2	27.6	20–33.1 (22)	3.9	39.7	35.1–41.9 (4)	3.2		
Anteroposterior diameter at the middle of the diaphysis	37.8	39	29.7–50.8 (17)	6.5	28.9	23.3–35.4 (22)	3.8	47.8	43.1–54 (4)	4.5		

^a Measurement from Richards et al. (1996), (Appendix B); –: not available.

Table 5

Comparative measurements (in mm) of immature bear humerus PC2-13 from Pellucidar Cave with Modern immature *Ursus arctos* and *U. americanus* humeri.

Measurement	<i>Ursus arctos</i> , Pellucidar Cave		<i>Ursus arctos</i> , Modern			<i>Ursus americanus</i> , Modern		
	PC2-13	Mean	Range (N)	SD	Mean	Range (N)	SD	
Minimum length of shaft from base of proximal articular surface to the capitulum	235.0	229.0	176–255 (5)	26.0	241.0	222–257 (9)	13.0	
Minimum transverse diameter of the diaphysis	21.5	24.27	18.3–27.24 (5)	3.45	23.52	18.16–27.47 (9)	2.79	
Minimum anteroposterior diameter of the diaphysis	21.5	28.28	17.5–35.75 (5)	6.9	24.23	21.63–28.96 (8)	2.16	
Minimum distal depth at trochlea	22.0	22.7	19.4–26.6 (5)	2.5	19.1	16.75–21.3 (9)	1.7	

fused distal epiphyses as in the Pellucidar specimen. Of four measurements, only the minimum distal depth at trochlea provided a clear indication of the species (**Table 5**). Ancient DNA analysis on the PC2-13 bone confirmed the identity of this specimen.

The left femur PC2-2 (**Fig. 3(3); Table 6**) is lacking the head and greater trochanter and shows damage at the distal end, particularly to the medial and lateral epicondyles. The specimen shows a strong medial ridge that extends proximally from above the medial condyle and does not appear rounded anteriorly, features consistent with *Ursus* (Merriam and Stock, 1925). In addition to these surface features, we assign this specimen to *U. arctos* based on three of four measurements on the PC2-2 femur that are consistent with adult brown bear. Only the minimum transverse diameter of the diaphysis overlaps with modern black bears in our sample (**Table 6**). The PC2-2 identification as *U. arctos* is additionally confirmed with genetic analysis.

4.2. Radiocarbon results

Six AMS radiocarbon age estimates and calibrated age ranges on the Pellucidar Cave bear specimens are shown in **Table 1**. Age estimates on brown bear (*U. arctos*) specimens are:

- Left humerus PC2-11: $12,440 \pm 35$ BP = 14,888–14,239 cal. BP (UCIAMS 41051);
- Femur PC2-2: $12,425 \pm 35$ BP = 14,836–14,211 cal. BP (UCIAMS 41050);
- Right humerus PC2-13: $11,110 \pm 30$ BP = 13,082–12,845 cal. BP (UCIAMS 41052).

Age estimates on giant short-faced bear (*A. simus*) specimens are:

- M2 PC2-1a: $11,720 \pm 50$ BP = 13,715–13,440 cal. BP (OxA 24005);
- Humerus PC2-3: $11,775 \pm 30$ BP = 13,725–13,477 cal. BP (UCIAMS 41048);
- Palatine PC2-1c: $11,615 \pm 30$ BP = 13,557–13,379 cal. BP (UCIAMS 41049).

The giant short-faced bear M2 and Humerus age estimates are statistically the same at the 95% confidence level, as are age estimates for the palatine and M2. The palatine is statistically significantly younger than that of the humerus, although statistical similarity in the ages of the humerus and M2, and the palatine and M2, along with the lack of duplication of bone elements, similar ontogeny, color, condition of preservation, and proximity of these bone specimens at the fossil site suggest only one individual is present. Combined age estimates for the three giant short-faced bear specimens give a calibrated age range of 13,572–13,458 cal. BP with a median age of 13,517 cal. BP. We also report one AMS age estimate on an *Ursus americanus* partial cranium from northern Vancouver Island that gave an age estimate of $11,935 \pm 40$ BP = 13,964–13,575 cal. BP (SC-1; UCIAMS 56479).

4.3. Ancient DNA analysis

Genetic analyses confirmed the assignment of specimens PC2-2, PC2-11 and PC2-13 as brown bear *Ursus arctos*. The DNA sequences for these specimens are 99% the same over the short region tested and match sequences from two different Canadian brown bear specimens available in GenBank: AF303110 (Delisle and Strobeck, 2002) and HE657204 (Hailer et al., 2012). For comparison, if the BLAST search was forced against the black bear *Ursus americanus* Pallas, 1780, PC2-13 was only 84% similar. Phylogenetic analysis strongly supports the Pellucidar Cave brown bear as belonging to Clade 4 (Bayesian posterior probability = 0.90; **Fig. 4**), with all southern Canadian and continental U.S.A. brown bears. We recover a time to most common ancestor for this clade to be ~56 ka BP (95% confidence interval: 36.0–88.6 ka BP). The common ancestor of the Pellucidar Cave individuals is estimated to be ~25.4 ka BP (13.9–36.6 ka BP; **Fig. 4**).

No genetic identification could be made for the giant short-faced bear specimen PC2-3. Cloning of the only PCR amplification that could be achieved resulted in a variety of bacterial sequences, indicating that there is likely no surviving DNA in this fossil specimen.

Table 6

Comparative measurements (in mm) of bear femur PC2-2 from Pellucidar Cave with Modern *Ursus arctos* and *U. americanus* and Pleistocene *Arctodus simus* femora.

Measurement	<i>Ursus arctos</i> , Pellucidar Cave		<i>Ursus arctos</i> , Modern			<i>Ursus americanus</i> , Modern			<i>Arctodus simus</i> , Pleistocene		
	PC2-2	Mean	Range (N)	SD	Mean	Range (N)	SD	Mean	Range (N)	SD	
Greatest length of complete specimens	–	418.0	352–534 (10)	61.0	324.0	282–381 (14)	27.0	558.1	490–723 ^a (14)	–	
Minimum length from trochanteric fossa to the intercondylar fossa	358.0	351.0	306–446 (14)	37.4	284.0	243–336 (15)	26.0	440.0	440 (approx.)	–	
Greatest breadth at proximal end	–	107.73	83.6–124.4 (10)	19.7	76.4	73.5–88 (14)	7.0	126.5	122 ^b –131 ^b	6.4	
Minimum transverse diameter of the diaphysis	32.2	37.4	27.7–52.2 (14)	6.4	27.5	23.4–32.7 (15)	3.2	43.2	42.2–44.1 ^b (3)	–	
Minimum anteroposterior diameter of the diaphysis	27.8	29.5	24.1–38.8 (14)	4.6	21.7	18.8–25 (15)	2.0	33.8	32.7–35	1.6	
Greatest breadth of the distal end	–	88.6	73.4–113 (10)	13.1	62.0	55.8–69 (14)	5.0	117.7	99–152 ^a (14)	–	
Minimum depth at centre of distal articular surface	45.7	47.4	39.9–62.1 (14)	6.2	36.9	33.3–42.9 (15)	3.1	52.3	47.4–55.6 (3)	–	

^a Measurements from Richards et al. (1996), Appendix B;

^b Measurements from Kurtén (1967); –: not available.

5. Discussion

5.1. Identification and genetic analysis

Differentiating species of bears with bone specimens from North American contexts can be challenging. Although there are morphological characters that separate *Ursus* from *Arctodus* (Merriam and Stock, 1925; Kurtén, 1967; Kurtén and Anderson, 1980), measurements in this study and others (Christiansen, 1999) show that differentiating these bears is not always possible based on size alone. Similarly, modern brown bears are generally larger than black bears, though size does not separate these bears completely. Identifying fossils of these ursid species is additionally confounded by the larger body size of Pleistocene than modern black bears, as noted by Kurtén and Anderson (1980) and as further examined by others (Gordon, 1986; Nagorsen et al., 1995; Graham, 1991; Wolverton and Lyman, 1998).

When morphological characteristics and measurements of fossil specimens do not differentiate bears to the species level, the use of genetic techniques on bones can be beneficial. Genetic analyses may be particularly useful for identifying well-preserved specimens from late Pleistocene sites in the contiguous U.S.A., where the possibility of misattributed bear fossils appears to be more acute now that brown bears are known to have migrated south to the contiguous U.S.A. from Eastern Beringia (Matheus et al., 2004; Davison et al., 2011) before the LGM (Clark et al., 2009), where only giant short-faced and black bears were previously thought to occur (Kurtén and Anderson, 1980).

Genetic analyses on fossil specimens can also reveal biological and biogeographic relationships within a species. Our genetic results on brown bears from Vancouver Island place them in Clade 4 with the North American brown bears that last appear in Alaska around 36 ka BP, which is consistent with the migration of the species southward from Beringia prior to the LGM. All three Pellucidar specimens fall within the mitochondrial genetic diversity of extant brown bears from southern Canada and the contiguous U.S.A., differing from those Clade 3b individuals found to the north and in central B.C. The brown bear remains from Pellucidar Cave belonged to populations that entered the contiguous U.S.A. before the LGM and moved to Vancouver Island from the east or south and not from the north along the coast.

5.2. Co-occurrences of *A. simus* and *U. arctos*

Radiocarbon results comparing brown and giant short-faced bears in Pellucidar Cave present an interesting perspective on the two species.

Based on an association of giant short-faced bears and brown bears at Little Box Elder Cave, Wyoming, Kurtén and Anderson (1974) proposed that giant short-faced bears may have been out-competed by brown bears as the latter expanded from eastern Beringia southward. Bones of both species have now also been reported from Alaska before ~34 ka BP (Kurtén and Anderson, 1980; Matheus, 1995; Barnes et al., 2002; Harrington, 2003; Matheus et al., 2004); in later Pleistocene deposits at Maricopa, California (Lundelius et al., 1983; Jefferson, 1991); and in Labor-of-Love Cave, Nevada (Emslie and Czaplewski, 1985). These data suggest that at times prior to the extinction of giant short-faced bears the two species occurred in overlapping geographic areas as brown bears spread throughout North America.

At Pellucidar Cave, age estimates on giant short-faced bear specimens indicate the species' presence on Vancouver Island at ~11.7 ka BP (~13.5 cal. ka BP). Brown bear specimens from the same cave date to soon before ($12,440 \pm 35$, $12,425 \pm 30$ BP; ~14.5 cal. ka BP) and after this age ($11,100 \pm 30$ BP; ~13 cal. ka BP), but without temporal overlap with giant short-faced bears. An age

estimate of $12,370 \pm 35$ BP (~14.39 cal. ka BP; Steffen, 2016) on brown bear from the nearby Arch-2 Cave is consistent with the earliest brown bears from Pellucidar Cave. The individuals of the two species tested here did not live in the same cave at the same time. However, as few as 300–500 calendar years separate them, supporting that both species were present in the Vancouver Island area during the latest Pleistocene.

Although it is difficult to say for certain based on the available fossil record, the non-overlapping occurrences of brown and short-faced bears at Pellucidar Cave could be interpreted as niche partitioning to reduce territorial competition in these sympatric species.

5.3. Bone damage

Several of the Pellucidar bone specimens show damage consistent with carnivore gnawing (Figs. 2, 3). G. Haynes (1983) differentiated gnawing damage to ungulate limb bones by extant large mammalian carnivores. He observed that tooth markings in trabecular bone, which often are most visible near long bone ends, typically are flat and square or rectangular when produced by bears, cone or truncated cone in canids and hyenas, and elongate V-shape in felids (G. Haynes, 1983; table 3). Although *A. simus* has carnassials with pointed cusps and shearing attributes so that tooth impressions from these bears can be expected to differ from those of extant ursine bears, no differences may be apparent in bears with worn or broken dentition. Based on these criteria, gnawing damage to the Pellucidar specimens is consistent with that of bears, the only confirmed large terrestrial carnivores on Vancouver Island during the late Pleistocene. A tooth impression on giant short-faced bear cranial fragment PC2-7 (Fig. 2(6)) is rectangular to oval in shape, and ~19 mm long by ~9 mm wide. The impression displays cusp marks consistent with the protoconid and the hypoconid on the trigonid and talonid of a bear m1, and could be from *Ursus* or *Arctodus*. Gnawing impressions on the head of the brown bear humerus (PC2-11; Fig. 3(1)) are flat-bottomed and up to 20 mm wide, indicating bears as a possible source of this damage. The condition of the epicondyles, greater trochanter and head of the brown bear femur (PC2-2; Fig. 3(3)) are also consistent with damage by bears. Irregular edges of the giant short-faced bear cranial fragments PC2-1 (Fig. 2(1, 2, 4)) and the distal end of humerus PC2-3 (Fig. 2(5)) may have resulted from carnivore gnawing, although there are no clear isolated tooth impressions on these specimens and breakage could have resulted from other sources such as crushing by roof fall. Spiral fracturing of distal humerus PC2-3 and the mid-shaft transverse/oblique break on PC2-11 occurred before substantial bone weathering (Behrensmeyer, 1978). The moist and cool environment in the cave may have delayed drying and cracking of bones such that these fractures could have occurred some time after the death of these animals.

Because giant short-faced bears have often been regarded as active agents in bone destruction (Kurtén, 1967; Guthrie, 1988; Voorhies and Corner, 1986; Gillette and Madsen, 1992) that break bones more readily than would typically be expected of extant bears (G. Haynes, 1983), it is conceivable that giant short-faced bears were a source of bone damage in this assemblage. Further, the non-contemporaneity of *Ursus* and *Arctodus* at the Pellucidar locality along with damage on the bones of both bears allows that this damage could have resulted from the same bear species as the specimen. With available information, however, it is impossible to determine which bear or bears might have been the source.

5.4. Fauna and vegetation

Faunal and vegetation changes that occurred around the end of the Pleistocene are likely factors in the extirpation of giant short-faced bears from Vancouver Island. When these bears were on

south Vancouver Island ~27.1 cal. ka BP ($22,750 \pm 140$ BP) they occupied a high trophic level in an open vegetation regime (Steffen and Harington, 2010) along with other large mammals (Harington, 1975) such as the mammoth *Mammuthus columbi* (including *M. imperator*) Falconer, 1857, mastodon *Mammut americanum* Kerr, 1792, and helmeted muskox *Bootherium bombifrons* Harlan, 1825. During the final stages of glaciation along coastal B.C., ice sheets grew to their maximum extent across much of Vancouver Island at ~17.4 cal. ka BP (14.5 ka BP), and then retreated rapidly (Porter and Swanson, 1998; Clague and James, 2002). Giant short-faced bears reinvaded Vancouver Island with a more modern fauna that included bison *Bison antiquus* (Leidy, 1852; Harington, 1975; Wilson et al., 2009) on southern Vancouver Island, as well as mountain goat *Oreamnos americanus* de Blainville, 1816 (Nagorsen and Keddie, 2000; Al-Suwaidi et al., 2006), brown bear (Steffen, 2016), and black bear ($11,935 \pm 40$ BP, ~13.76 cal. ka BP; UCIAMS 56479) on northern Vancouver Island. Of these large mammals, only the black bear remained on the island through the Holocene.

Vegetation shifts at the end of the Pleistocene may have been unfavorable for giant short-faced bears. Coincident with the ~13.5 cal. ka BP (~11.7 ka BP) age of the giant short-faced bear remains, vegetation changed rapidly from open woodlands with abundant lodgepole pine *Pinus contorta* to increasingly closed forests with shade-tolerant spruce *Picea*, mountain hemlock *Tsuga mertensiana*, and red alder *Alnus rubra*. Increases in lodgepole pine, green alder *A. crispa*, and mountain hemlock ~12.6 to ~12.3 cal. ka BP (~10.6 to ~10.4 ka BP) point toward cool and moist conditions during the Younger Dryas stadial (Mathewes, 1993; Lacourse, 2005). Closed forests expanded into the early Holocene with western hemlock *Tsuga heterophylla* becoming dominant (Lacourse, 2005). The extirpation of many large mammals from Vancouver Island along with the vegetation shift to a closed forest regime at the end of the Pleistocene likely contributed to the local extirpation of giant short-faced bears by reducing the amount or quality of forage for its subsistence.

5.5. Diet and ecology

The ecology of giant short-faced bears informs their occurrence at the fossil locality. Typically characterized as an open adapted species (Kurtén and Anderson, 1980; Harington, 1973; Matheus, 2003; Churcher et al., 1993; Richards et al., 1996), the distribution of giant short-faced bears indicates its occupation of diverse settings (Schubert et al., 2010). Even though these bears were not restricted to open areas and could occur in different environments, the timing of the regional shift from an open pine woodland habitat to a densely forested vegetation regime with the occurrence of the giant short-faced bear remains at Pellucidar Cave implies that these vegetation changes contributed to the local extirpation of this species.

Giant short-faced bears have been characterized on morphological grounds as carnivorous and possibly active predators (Kurtén, 1967; Harington, 1996; Kurtén and Anderson, 1980; Voorhies and Corner, 1986; Agenbroad, 1990; Guthrie, 1988; Gillette and Madsen, 1992; Churcher et al., 1993; Richards et al., 1996). These bears have also been described as strict scavengers with functional morphology suited to long-distance procurement of carcasses (Matheus, 2003), and as omnivorous (Baryshnikov et al., 1994; Sorkin, 2006) with flexible diets that varied according to resource availability similar to extant brown bears (Figueirido et al., 2010). The perspectives have also been offered by comparison with its closest living relative the South American spectacled bear *Tremarctos ornatus* Gervais, 1855, that giant short-faced bears had omnivorous diets based on dental wear (Donohue et al., 2013), and mainly vegetation diets based on morphological

similarities (Emslie and Czaplewski, 1985; Meloro, 2011). Overall, recent literature provides little evidence that giant short-faced bears were primarily active carnivores or strictly vegetarian, and instead indicates that these bears were omnivores with scavenging tendencies.

Though giant short-faced bear diets may have varied regionally and through time, regular consumption of animal matter by these bears is supported by the presence of carnassial teeth with sheering attributes and a low jaw condyle relative to the tooth row (Kurtén, 1967; Voorhies and Corner, 1986). Meat consumption is confirmed by elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in numerous late Pleistocene giant short-faced bear specimens from the northern part of their range, where these bears may have competed for food but usually occupied a higher trophic level compared with invading brown bears (Bocherens et al., 1995; Matheus, 1995; Barnes et al., 2002; Fox-Dobbs et al., 2008). That giant short-faced bears may have excluded brown bears from Eastern Beringia from ~34 to ~20 ka BP further suggests these large bears may typically have been dominant over brown bears.

Competition amongst bears may have increased as food resources shifted at the end of the Pleistocene, as our age estimates suggest giant short-faced bears temporarily displaced brown bears from the Pellucidar Cave area. As glaciers receded from this region at the end of the Pleistocene there may have been a relatively brief time when environmental conditions met the habitat and dietary requirements of giant short-faced bears. These requirements are likely to have included the existence of sufficient animal matter for subsistence as scavenged carcasses and possibly as prey. Giant short-faced bears could range widely for available forage (Kurtén, 1967; Matheus, 2001) and may have occupied and then left post-glacial Vancouver Island with the boom-and-bust availability of preferred habitat and foods as faunal turnover resulted in available carrion. When closed forests encroached and large meat packages dwindled, giant short-faced bears declined and brown bears recurred. Post-glacial shifts in available resources may also have promoted the eventual extirpation of brown bears from the island, though, unlike giant short-faced bears, brown bears persisted in adjacent areas (Mustoe et al., 2005). Greater dietary and habitat plasticity (Kurtén, 1967; Matheus, 1995) could have facilitated the persistence of brown bears and not of giant short-faced bears as environments changed abruptly toward the Holocene in this region.

On a continent-wide scale our perspective from Pellucidar Cave offers that brown and short-faced bears were sympatric at times as brown bears spread through North America. Our data and others support that giant short-faced bears may typically have dominated competitive interactions, particularly when their populations were robust, and displaced brown bears from specific localities. We suggest that at the end of the Pleistocene one reason brown bears persisted where giant short-faced bears died off is because giant short-faced bears may have been less flexible in adapting to new and rapidly changing environments that impacted the availability or quality of food and possibly habitat. Future studies of the trophic interactions of these bear species may show if competition is likely to have contributed to the changing availability of food resources for giant short-faced bears.

5.6. Implications for early people in the Americas

Occurrences of brown and short-faced bears on Vancouver Island have implications for early human occupation. The timing and routes of early people in the Americas are enduring archaeological questions. Unequivocal archaeological evidence from Monte Verde in Chile dated to ~15 cal. ka BP (~12.5 ka BP; Dillehay, 1997) as well as from Swan Point in central Alaska, and a handful of other early archaeological sites indicate that people had

colonized North and South America by ~15–14 cal. ka BP (Yesner, 2001; Madsen, 2004, 2015; Goebel et al., 2008; Meltzer, 2009). Recent radiocarbon age estimates on cut-marked bones from Bluefish Caves in the Yukon Territory show a human presence as early as 24,000 cal. BP ($19,650 \pm 130$ ^{14}C BP; Bourgeon et al., 2017). An earlier find of a flaked mammoth bone radiocarbon dated to 24,000 BP has also been described from Bluefish Caves (Harington and Cinq-Mars, 2008). Together these data support a Beringian standstill hypothesis that suggests a small human population became isolated in Eastern Beringia and dispersed southward near the end of the LGM (Tamm et al., 2007; Mulligan et al., 2008; Raghavan et al., 2015; Llamas et al., 2016). Peak glacial conditions and a coalescence of the Cordilleran and Laurentide ice sheets east of the Rocky Mountain Range from approximately 24 to 14 cal. ka BP (~20 and ~12 ka BP) is likely to have provided no passageway for humans between eastern Beringia and the contiguous U.S.A. (Clague et al., 2004; Dyke, 2004; Pedersen et al., 2016). Coastlines west of the Cordilleran Ice Sheet in Southeast Alaska and B.C. were deglaciated before 15 cal. ka BP, included glacial refugia, and could have been a way that people dispersed southward (Heusser, 1960; Fladmark, 1979; Werner et al., 1982; Luternauer et al., 1989; Josenhans et al., 1995; Hebda et al., 1997; Barrie and Conway, 1999; Byun et al., 1999; Mandryk et al., 2001; Al-Suwaidi et al., 2006; Clague et al., 2004; Fedje and Mathewes, 2005; Carrara et al., 2007; Mackie et al., 2011; McLaren et al., 2014; Mathewes et al., 2015; Steffen, 2016). There has been much discussion about the timing and viability of the west coast refugium as a route for early people. The biological productivity of this region and the potential availability of food resources are part of these discussions.

The presence of large carnivores – brown and short-faced bears – indicates that the terrestrial environment of north Vancouver Island was a productive ecosystem between 14.7 and 12.95 cal. ka BP. Although people have abilities and technological capacities that can draw different affordances from environments than do bears, the presence of these carnivores indicates ecological conditions that could support people. Our data add to previous ages on large mammal fossils along the west coast, including mountain goat bones dated to 19.7 and 14.3 cal. ka BP ($16,340 \pm 60$ BP and $12,340 \pm 50$ BP) that flank glacial sediments at Port Eliza Cave on the west coast of Vancouver Island (Al-Suwaidi et al., 2006), and brown bears dated to ~17.5 and ~13.1 cal. ka BP ($14,390 \pm 70$ BP and $11,250 \pm 70$ BP) that indicate productive biological environments on Haida Gwaii (Mackie et al., 2011). Small mammals including deer mouse (*Peromyscus*; Gloger, 1841) and heather vole (*Phenacomys*; Merriam, 1889) were also present on post-glacial north Vancouver Island by ~13.8 cal. ka BP ($11,960 \pm 45$ BP; Steffen, 2016). The radiocarbon ages of the Vancouver Island bear specimens are additionally informative as they are older than the ages of large mammals documenting an ecologically productive corridor between the ice sheets after the LGM (Burns, 1996; Zazula et al., 2009), including age estimates on bison specimens dated to ~13.4 cal. ka BP (~11.5 ka BP) (Heintzman et al., 2016; see also Pedersen et al., 2016).

In addition to informing the availability of coastal landscapes for human occupation by nearly 15 ka BP, this study highlights the biogeographic passage of large terrestrial mammals south from Eastern Beringia before the LGM. Brown bears, woolly mammoths and steppe bison likely reached the southern refugium in the unglaciated U.S.A. during the mid-Wisconsin ice-free period. That route may have been feasible for humans as well (Harington, 2012), though the timing of these migrations may be too early to be directly relevant to human entry into the middle and southern latitude Americas (Goebel et al., 2008; but see Holen et al., 2017 for last interglacial age signs of people from southern California).

Humans moving into North America may have found large Pleistocene carnivores such as giant short-faced bears to be a barrier to gaining a foothold (Geist, 1989; but see Matheus, 2001).

In addition to being the largest and most powerful carnivorous land mammals in North America, giant short-faced bears were capable of bursts of speed and had locomotor capabilities for obtaining distant subsistence resources (Harington, 1996; Matheus, 2003). Geist (1989) suggested that humans entering the Americas, though familiar with brown bears, would not have been able to effectively contend with the giant short-faced bear and other large Pleistocene carnivores, a situation that would have suppressed human population expansion. Geist's (1989) perspective, which explicitly refutes the notion of human supremacy in the ecology of Pleistocene North America and contrasts the hypothesis that large Pleistocene mammals were hunted to extinction as first peoples expanded through the continent (Martin, 1967), finds some support in the late Pleistocene record. Before the extinction of many Pleistocene mammals, people were thinly spread throughout the Americas with diverse archaeological lithic technologies including Clovis, Western Stemmed, and Fishtail traditions (Madsen, 2015). There is no strong evidence, however, that these people hunted large extinct Pleistocene carnivores, including no clear indication of direct human involvement in the extinction of giant short-faced bears (Faith and Surovell, 2009; Grayson and Meltzer, 2015: table 3). It is clear that people were at least occasionally involved in the death and/or butchery of several different large non-carnivorous Pleistocene mammals, particularly mammoths and mastodons (C.V. Haynes, 1964; Grayson and Meltzer, 2015), which may at times have put people in competition with giant short-faced bears for carcasses and possibly for prey. Defense against these large bears as well as abandonment of carcasses are plausible outcomes. Indeed, the relationship of people to giant short-faced bears is likely to have been uneasy at best.

Defining the causes of North American late Pleistocene extinctions has long been challenged by the need to separate the coincident occurrences of climate change and an expanding human presence, and of sorting out the consequences of these and other possible factors. Because the diversity of ecological responses to such factors in numerous extinct genera is potentially vast, we suggest seeking the effects that specific proximal causes may have had on such taxa in particular contexts leading up to extinction is a reasonable path toward understanding North American Quaternary extinctions as a whole. In this study, we examined the effects of competition with brown bears on giant short-faced bears in the context of vegetation and faunal change on Vancouver Island near the end of the Pleistocene. In doing so we hope to have contributed to this objective.

6. Conclusions

We provided an account of the late Pleistocene distributions of brown bears and giant short-faced bears in western North America based on rare fossils of these bears from Vancouver Island, and we discussed these remains in terms of the competition hypothesis for the extinction of giant short-faced bears. A partial cranium and the distal portion of the shaft of a left humerus from the Pellucidar Cave fossil locality are referred to the giant short-faced bear *Arctodus simus*. Radiocarbon dates on these bones indicate that this species lived around the cave at ~13.5 cal. ka BP. Part of a left humerus, a right humerus of an immature individual, and a left femur are referred to the brown bear *Ursus arctos*. Ancient DNA analysis indicates that brown bears residing on Vancouver Island near the end of the Pleistocene arrived from the east or south as they share ancestry with modern-day Clade 4 brown bears that are prominent in the contiguous U.S.A. but do not occur in B.C. north of the fossil site. Our radiocarbon ages indicate that brown bears lived at Pellucidar Cave at ~14.5 cal. ka BP and ~13 cal. ka BP. Together these radiocarbon ages suggest that competition was possible

between brown and giant short-faced bears and may have resulted in niche partitioning for territory and cave use.

Post-glacial faunal and vegetation shifts changed the foraging options available to these large carnivores and are likely to have contributed to the arrival and the local extirpation of giant short-faced bears from Vancouver Island. A higher degree of dietary and habitat flexibility and possibly a comparatively smaller foraging radius than that of giant short-faced bears are likely to have facilitated brown bears persistence in the broader region into the Holocene. In terms of early human occupation in the Americas our study documents the existence of a robust ecosystem on north Vancouver Island that was available for human occupation, supporting the west coast as an option for early human occupation and migration.

Our paleontological and radiocarbon data on bear fossils from Pellucidar Cave together with the application of *aDNA* methods, as well as paleoecological and archaeological sources have provided some of the necessary details for defining how changes on the landscape, including competition with brown bears, may have affected giant short-faced bears leading up to their extinction. We show that changing species interactions can be considered in Pleistocene extinctions, and we highlight that rapid shifts in the availability or quality of food and habitat are likely to have been important in the extinction of giant short-faced bears.

Acknowledgments

Supplementary data available in Appendix B have also been deposited in a Dryad data package under the <https://doi.org/10.5061/dryad.f26g1>. DNA sequences are deposited in GenBank under the accession numbers JX448567–JX448569.

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Appendix A. List of comparative material referenced in Tables 2–6

Institutional Abbreviations: CMN, Canadian Museum of Nature, Gatineau, Quebec, Canada; LACM, Los Angeles County Museum, Los Angeles, California, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; RBCM, Royal BC Museum, Victoria, Canada; UCMP, Museum of Paleontology, University of California, Berkeley, California, USA.

Table 2. P4–M2, *Arctodus simus*: UCMP 3001, UCMP 3005, UCMP 3007, UCMP 3014, UCMP 8511. I1: UCMP 3001, UCMP 3857, UCMP 3924, UCMP 4001, UCMP 4130.

Table 3. Distal humerus, *Arctodus simus*: UCMP 3039, UCMP 3039, UCMP 3748, UCMP 3351; *Ursus americanus*: LACM 30855, MVZ 13764, MVZ 30116. Complete humeri, *Ursus americanus*: MVZ 682, MVZ 12845, MVZ 13764, MVZ 14712, MVZ 30116, MVZ 30586, MVZ 30855, MVZ 43896, MVZ 50251, MVZ 86009, MVZ 88906, MVZ 80754, MVZ 80756, MVZ 81580, MVZ 81581, MVZ 94806, MVZ 101698.

Table 4. Proximal humeri, *Ursus arctos*: CMN 2772, CMN 3979, CMN 31187, LACM 625, LACM 30466, LACM 30586, LACM 31266,

MVZ 970, MVZ 4385, MVZ 24537, MVZ 24538, MVZ 50250, MVZ 99747, MVZ 184151, MVZ 123990, RBCM 10401, RBCM 11163; *Ursus americanus*: CMN 1583, CMN 5009, CMN 28653, CMN 38268, LACM 682, LACM 86009, LACM 88906, MVZ 12845, MVZ 13764, MVZ 14712, MVZ 30116, MVZ 30855, MVZ 43896, MVZ 50251, MVZ 80754, MVZ 80756, MVZ 81581, MVZ 81580, MVZ 94806, MVZ 101698, RBCM 4884, RBCM 6970; *Arctodus simus*: UCMP 3039, UCMP 3039, UCMP 3351, UCMP 3748.

Table 5. Humerus, *Ursus arctos*: CMN 75113, MVZ 125562, MVZ 43895, MVZ 24408, RBCM 10031, RBCM 9776; *Ursus americanus*: CMN 75345, MVZ 4763, MVZ 4367, MVZ 12460, MVZ 81581, MVZ 116827, MVZ 31968, RBCM 9047, RBCM 10212.

Table 6. Femur, *Ursus arctos*: CMN 41056, MVZ 970, MVZ 4385, MVZ 24537, MVZ 30116, MVZ 99747, MVZ 123990, MVZ 184151, LACM 625, LACM 30466, LACM 31266, RBCM 9277, RBCM 10401, RBCM 11163; *Ursus americanus*: CMN 75573, LACM 682, LACM 30855, LACM 88906, LACM 86009, MVZ 14712, MVZ 43896, MVZ 70340, MVZ 80754, MVZ 80756, MVZ 81580, MVZ 81581, MVZ 94806, RBCM 4884, RBCM 6970; *Arctodus simus*: UCMP 3721, UCMP 10211, UCMP 10212.

Appendix B. Supplementary data

Supplementary information (including Figs. S1, S2 and Table S1) associated with this article can be found, in the online version, at: <https://doi.org/10.1016/j.geobios.2017.12.001>.

References

- Agenbroad, L.D., 1990. The mammoth population of the Hot Springs Site and associated megafauna. In: Agenbroad, L.D., Mead, J.I., Nelson, L.W. (Eds.), *Megafauna and man: discovery of America's heartland*, 1, The Mammoth Site of Hot Springs, South Dakota, Inc., Scientific Papers, pp. 32–39.
- Al-Suwaidi, M., Ward, B.C., Wilson, M.C., Hebda, R.J., Nagorsen, D.W., Marshall, D., Gheble, B., Wigen, R.J., Enkin, R.J., 2006. Late Wisconsinan Port Eliza Cave sediments and their implications for human coastal migration, Vancouver Island Canada. *Gearcheology* 21, 307–332.
- Barbour, H., 1916. A giant Nebraska bear *Dinachitotherium merriami*. *Bulletin of the Nebraska Geological Survey* 4, 349–353.
- Barnes, I., Matheus, P., Shapiro, B., Jensen, D., Cooper, A., 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* 295, 2267–2270.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306, 70–75.
- Barrie, J.V., Conway, K.W., 1999. Late Quaternary glaciation and postglacial stratigraphy of the northern Pacific margin of Canada. *Quaternary Research* 51, 113–123.
- Baryshnikov, G., Agenbroad, L.D., Mead, J.I., 1994. Carnivores from the mammoth site, Hot Springs, South Dakota. In: Agenbroad, L.D., Mead, J.I. (Eds.), *The Hot Springs Mammoth Site*. Fenske Printing Inc, South Dakota, pp. 306–358.
- Beaumont, W., Beverly, R., Souton, J.R., Taylor, R.E., 2010. Bone preparation at the KCAMS laboratory. *Nuclear Instruments & Methods in Physics Research. Section B. Beam Interactions with Materials and Atoms* 268, 906–909.
- Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Bocherens, H., Emslie, S.D., Billiou, D., Mariotti, A., 1995. Stable isotopes (^{13}C , ^{15}N) and paleodiets of the giant short-faced bear (*Arctodus simus*). *Comptes rendus de l'Académie des Sciences, Serie 2, Sciences de la Terre et des planètes* 320, 779–784.
- Bourgeon, L., Burke, A., Higham, T., 2017. Earliest human presence in North America dated to the Last Glacial Maximum: new radiocarbon dates from Bluefish Caves, Canada. *PLoS ONE* 12, e0169486.
- Bowditch, T.E., 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris.
- Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337–360.
- Bronk Ramsey, C., Higham, T., Leach, P., 2004. Towards high-precision AMS: progress and limitations. *Radiocarbon* 46, 17–24.
- Brown, T.A., Nelson, D.E., Vogel, J.S., Souton, J.R., 1988. Improved collagen extraction by modified Longin method. *Radiocarbon* 30, 171–177.
- Burns, J.A., 1996. Vertebrate paleontology and the alleged ice-free Corridor: the meat of the Matter. *Quaternary International* 32, 107–112.
- Byun, S.A., Koop, B.K., Reimchen, T.E., 1999. North American black bear mtDNA phylogeography: implications for morphology and the Haida Gwaii glacial refugium controversy. *Evolution* 51, 1647–1653.

- Carrara, P.E., Ager, T.A., Baichtal, J.F., 2007. Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. Canadian Journal of Earth Sciences 44, 229–244.
- Christiansen, P., 1999. What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? Annales Zoologici Fennici 36, 93–102.
- Churcher, C.S., Morgan, A.V., Carter, L.D., 1993. *Arctodus simus* from the Alaskan Arctic Slope. Canadian Journal of Earth Science 30, 1007–1013.
- Clague, J.J., James, T.S., 2002. History and isostatic effects of the last ice sheet in southern British Columbia. Quaternary Science Reviews 21, 71–87.
- Clague, J.J., Mathews, R.W., Ager, T.A., 2004. Environments of northwestern North America before the Last Glacial Maximum. In: Madsen, D.B. (Ed.), Entering America: Northeast Asia and Beringia before the Last Glacial Maximum. University of Utah Press, Salt Lake City, pp. 63–94.
- Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. Science 325, 710–714.
- Cope, E.D., 1879. The cave bear of California. American Naturalist 13, 791.
- Cope, E.D., 1891. The California cave bear. American Naturalist 25, 997–999.
- Dalquest, W.W., Mooser, O., 1980. Late Hemphillian mammals of El Ocote local fauna, Guanajuato, México. Pearce-Sellards Series. Texas Memorial Museum 32, 1–25.
- Davison, J., Ho, S.Y.W., Bray, S.C., Korsten, M., Tammeleht, E., Hindrikson, M., Ostbye, K., Ostbye, E., Lauritzen, S., Austin, J., Cooper, A., Saarma, U., 2011. Late-Quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. Quaternary Science Reviews 30, 418–430.
- de Blainville, H., 1816. Prodrome d'une nouvelle distribution systématique du règne animal. Bulletin de la Société Philomathique 3, 113–124.
- Delisle, I., Strobeck, C., 2002. Conserved primers for rapid sequencing of the complete mitochondrial genome from carnivores, applied to three species of bears. Molecular Biology and Evolution 19, 357–361.
- Dillehay, T., 1997. Monte Verde: A late Pleistocene settlement in Chile Vol. 2: The archaeological context and interpretation. Smithsonian Institution Press, New York.
- Donohue, S.L., DeSantis, L.R.G., Schubert, B.W., Ungar, P.S., 2013. Was the giant short-faced bear a hyper-scavenger? A new approach to the dietary study of ursids using dental microwear textures. PLoS ONE 8, e77531.
- Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7, 214.
- Drummond, A.J., Rambaut, A., Shapiro, B., Pybus, O.G., 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. Molecular Biology and Evolution 22, 1185–1192.
- Dyke, A.S., 2004. An outline of North American deglaciation with emphasis on central and northern Canada. In: Ehlers, J., Gibbard, P.L. (Eds.), Quaternary Glaciations: Extent and Chronology, Part 2, North America. Elsevier, Amsterdam, pp. 371–406.
- Edwards, C.J.E., Suchard, M.A., Lemey, P., Welch, J.J., Barnes, I., Fulton, T.L., Barnett, R., O'Connell, T.C., Coxon, P., Monaghan, N., Valdiosera, C.E., Lorenzen, E.D., Wilwerslev, E., Baryshnikov, G.F., Rambaut, A., Thomas, M.G., Bradley, D.G., Shapiro, B., 2011. Ancient hybridization and an Irish origin for the modern polar bear matriline. Current Biology 21, 1251–1258.
- Emslie, S.D., 1995. Paleontology and geology of the Leisey Shell Pits, early Pleistocene of Florida. Bulletin Florida Museum of Natural History 37, 502–514.
- Emslie, S.D., Czaplewski, N., 1985. A new record of giant short-faced bear. *Arctodus simus*, from western North America with a re-evaluation of its paleobiology. Los Angeles County Museum Contributions in Science 371, 12.
- Faith, J.T., Surovell, T.A., 2009. Synchronous extinction of North America's Pleistocene mammals. Proceedings of the National Academy of Sciences of the United States of America 106, 20641–20645.
- Falconer, H., 1857. On the species of mastodon and elephant occurring in the fossil state in Great Britain, Part 1, Mastodon. Quaternary Journal of the Geological Society of London 13, 307–360.
- Fedje, D.W., Mathewes, R.W., 2005. Haida Gwaii: Human history and environment from the time of loon to the time of the iron people. UBC Press, Vancouver407p.
- Figueirido, B., Palmqvist, P., Pe, J.A., 2010. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. Journal of Zoology 277, 70–80.
- Fladmark, K.R., 1979. Routes: Alternate migration corridors for early man in North America. American Antiquity 44, 55–69.
- Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 30–46.
- Geist, V., 1989. Did large predators keep humans out of North America? In: Clutton-Brock, J. (Ed.), The walking larder: patterns of domestication, pastoralism, and predation. Unwin Hyman, London, pp. 282–294.
- Gervais, P., 1855. Recherches sur les mammifères fossiles de l'Amérique du Sud. In: Castelnau, F. (Ed.), Expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para, exécutée par ordre du Gouvernement français pendant les années 1843 à 1847 sous la direction de F. Castelnau. Bertrand, Paris, pp. 1–63.
- Gilbert, M.T.P., Bandelt, H.J., Hofreiter, M., Barnes, I., 2005. Assessing ancient DNA studies. Trends in ecology & evolution 20, 541–544.
- Gillette, D.D., Madsen, D.M., 1992. The short-faced bear *Arctodus simus* from the late Quaternary in the Wasatch Mountains of central Utah. Journal of Vertebrate Paleontology 12, 107–112.
- Gloger, C.W.L., 1841. Gemeinnütziges hand-und hilfsbuch der naturgeschichte: für gebildete leser aller stände. Band I. Schulz & Co, Breslau.
- Goebel, T., Waters, M.R., O'Rourke, D.H., 2008. The late Pleistocene dispersal of modern humans in the Americas. Science 319, 1497–1502.
- Gordon, K.R., 1986. Insular evolutionary body size trends in *Ursus*. Journal of Mammalogy 67, 395–399.
- Graham, R.W., 1991. Variability in the size of North American Quaternary black bears (*Ursus americanus*) with the description of a fossil black bear from Bill Neff Cave, Virginia. Illinois State Museum Scientific Papers 23, 238–250.
- Gray, J.E., 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of genera apparently appertaining to each tribe. Annals of Philosophy 10, 337–344.
- Grayson, D.K., 2007. Deciphering North American Pleistocene extinctions. Journal of Anthropological Research 63, 185–213.
- Grayson, D.K., 2015. Giant sloths and sabertooth cats: extinct mammals and the archaeology of the ice age Great Basin. University of Utah Press, Salt Lake City.
- Grayson, D.K., Meltzer, D.J., 2015. Revisiting Paleoindian exploitation of extinct North American mammals. Journal of Archaeological Science 56, 177–193.
- Guthrie, R.D., 1988. Bone litter from an Alaskan Pleistocene carnivore den. Current Research in the Pleistocene 5, 69–71.
- Hailer, F., Kutschera, V.E., Hallström, B.M., Klassert, D., Fain, S.R., Leonard, J.A., Arnason, U., Janke, A., 2012. Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage. Science 336, 344–347.
- Hänni, C., Laudet, V., Stehelin, D., Taberlet, P., 1994. Tracking the origins of the cave bear (*Ursus spelaeus*) by mitochondrial-DNA sequencing. Proceedings of the National Academy of Sciences of the United States of America 91, 12336–12340.
- Harington, C.R., 1973. A short-faced bear from ice age deposits at Lebret, Saskatchewan. The Blue Jay 31, 11–14.
- Harington, C.R., 1975. Pleistocene muskoxen (*Symbos*) from Alberta and British Columbia. Canadian Journal of Earth Sciences 12, 903–919.
- Harington, C.R., 1996. North American short-faced bear. Beringian Research Notes 4, 1–4.
- Harington, C.R. (Ed.), 2003. Annotated bibliography of Quaternary Vertebrates of Northern North America – with radiocarbon dates. University of Toronto Press, Toronto.
- Harington, C.R., Cinq-Mars, J., 2008. Bluefish Caves – fauna and context. Beringian Research Notes 19, 1–8.
- Harington, C.R., 2012. Quaternary cave faunas of Canada: a review of the vertebrate remains. Journal of Cave and Karst Studies 73, 162–180.
- Harlan, R., 1825. Fauna Americana: being a description of the mammiferous animals inhabiting North America. Anthony Finley, Philadelphia.
- Haynes, C.V., 1964. Fluted projectile points: their age and dispersion. Science 145, 1408–1413.
- Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9, 164–172.
- Hebda, R.J., Howes, D., Maxwell, B., 1997. Brooks Peninsula as an ice age refugium. In: Hebda, R.J., Haggarty, J. (Eds.), Brooks Peninsula, An ice age Refugium. Ministry of Environment, Lands and Parks, British Columbia Parks Occasional Paper no. 5, pp. 15.1–15.7.
- Heintzman, P.D., Froese, D., Ives, J.W., Soares, A.E.R., Zazula, G.D., Letts, B., Andrews, T.D., Driver, J.C., Hall, E., Hare, P.G., Jass, C.N., MacKay, G., Southon, J.R., Stiller, M., Woywitka, R., Suchard, M.A., Shapiro, B., 2016. Bison phylogeography constrains dispersal and viability of the Ice Free Corridor in western Canada. Proceedings of the National Academy of Sciences of the United States of America 113, 8057–8063.
- Heusser, C.J., 1960. Late-Pleistocene environments of North Pacific North America: an elaboration of late-glacial and post-glacial climatic, physiographic and biotic changes. Special Publication no. 35, American Geographical Society, New York.
- Holen, S.R., Deméré, T.A., Fisher, D.C., Fullagar, R., Paces, J.B., Jefferson, G.T., Beeton, J.M., Cerutti, R.A., Rountrey, A.N., Vescera, L., Holen, K.A., 2017. A 130,000-year-old archaeological site in southern California, USA. Nature 544, 479–483.
- Holland, S.S., 1976. Landforms of British Columbia. British Columbia Department of Mines Bulletin 48, 138.
- Howes, D.E., 1983. Late Quaternary sediments and geomorphic history of northern Vancouver Island. British Columbia: Canadian Journal of Earth Sciences 20, 57–65.
- Jefferson, G., 1991. A catalogue of late Quaternary vertebrates from California: Part two Mammals. Natural History Museum of Los Angeles Technical Report No. 7, Los Angeles.
- Josenhans, H.W., Fedje, D.W., Conway, K.W., Barrie, J.V., 1995. Post glacial sea levels on the Western Canadian continental shelf: evidence for rapid change, extensive subaerial exposure, and early human habitation. Marine Geology 125, 73–94.
- Kerr, R., 1792. The Animal Kingdom, or Zoological Systems of the Celebrated Sir Charles Linnaeus. J. Murray and R. Faulder, London.
- Kurtén, B., 1967. Pleistocene bears of North America. Pt. 2 Genus *Arctodus*, short-faced Bears. Acta Zoologica Fennica 117, 60.
- Kurtén, B., Anderson, E., 1974. Association of *Ursus arctos* and *Arctodus simus* (Mammalia: Ursidae) in the late Pleistocene of Wyoming. Breviora 426, 1–6.
- Kurtén, B., Anderson, E., 1980. Pleistocene mammals of North America. Columbia University Press, New York.
- Lacourse, T., 2005. Late Quaternary dynamics of forest vegetation on northern Vancouver Island, British Columbia, Canada. Quaternary Science Review 24, 105–121.

- Lambe, J.M., 1911. On *Arctotherium* from the Pleistocene of Yukon. Ottawa Naturalist 25, 21–26.
- Leidy, J., 1852. Memoir on the extinct species of American Ox. Smithsonian Contributions to Knowledge 5 (3), 20.
- Leidy, J., 1854. Remarks on *Sus americanus*, or *Harlanus americanus* and on other extinct mammals. Proceedings of the Academy of Natural Sciences of Philadelphia 7, 89–90.
- Leonard, J.A., Wayne, R.K., Cooper, A., 2000. Population genetics of ice age brown bears. Proceedings of the National Academy of Sciences of the United States of America 97, 1651–1654.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*, 10th edition. Laurentius Salvius, Stockholm 824.
- Llamas, B., Frenschmidt, L., Valverde, G., Soubrier, J., Mallick, S., Rohland, N., Nordenfelt, S., Valdiosera, C., Richards, S.M., Rohrlach, A., Barreto Romero, M.I., Espinoza, I.F., Tomasto Cagigao, E., Watson Jiménez, L., Makowski, K., Lebreiro Reyna, I.S., Mansilla Lory, J., Ballivián Torrez, J.A., Rivera, M.A., Burger, R.L., Ceruti, M.C., Reinhard, J., Wells, R.S., Politis, G., Santoro, C.M., Standen, V.G., Smith, C., Reich, D., Ho, S.Y.W., Cooper, A., Haak, W., 2016. Ancient mitochondrial DNA provides high-resolution time scale of the peopling of the Americas. Science Advances 2, e1501385.
- Lundelius Jr., E.L., Graham, R.W., Anderson, E., Guilday, J., Holman, A., Steadman, D.W., Webb, S.D., 1983. Terrestrial vertebrate faunas. In: Porter, C.S. (Ed.), Late Quaternary Environments of the United States, Volume 1, The late Pleistocene. University of Minnesota Press, Minneapolis, pp. 211–235.
- Luernauer, J.L., Clague, J.J., Conway, K.W., Barrie, J.V., Blaise, B., Mathews, R.W., 1989. Late Pleistocene terrestrial deposits on the continental shelf of western Canada: evidence for rapid sea level change at the end of the last glaciation. Geology 17, 357–360.
- McLaren, D., Fedje, D., Murray, B.H., Mackie, Q., Walker, I.J., Shugar, D.H., Eamer, J.B.R., Lian, O.B., Neudorf, C., 2014. A post-glacial sea level hinge on the central Pacific coast of Canada. Quaternary Science Reviews 97, 148–169.
- Mackie, Q., Fedje, D., McLaren, D., Smith, N., McKechnie, I., 2011. Early environments and archaeology of coastal British Columbia. In: Bicho, N.F., Haws, J.A., Davis, L.G. (Eds.), Trekking the shore: changing coastlines and the antiquity of coastal settlement. Springer-Verlag, New York, pp. 51–103.
- Madsen, D.B., 2000. A high-elevation Allerød-Younger Dryas megafauna from the west-central Rocky Mountains. In: Madsen, D.B., Metcalf, M.D. (Eds.), Intermountain archaeology. University of Utah Anthropological Papers no. 122, Salt Lake City, pp. 100–113.
- Madsen, D.B., 2004. Entering America Northeast Asia and the Beringia before the Last Glacial Maximum. University of Utah Press, Utah.
- Madsen, D.B., 2015. A framework for the initial occupation of the Americas. PaleoAmerica 1, 217–250.
- Mandryk, C.A.S., Josenhans, H., Fedje, D.W., Mathewes, R.W., 2001. Late Quaternary paleoenvironments of Northwestern North America: implications for inland versus coastal migration routes. Quaternary Science Reviews 20, 301–314.
- Martin, P.S., 1967. Prehistoric overkill. In: Martin, P.S., Wright, Jr., H.E. (Eds.), Pleistocene extinctions: the search for a cause. Yale University Press, New Haven, pp. 75–120.
- Mathewes, P.E., 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. Quaternary Research 44, 447–453.
- Mathewes, P.E., 2001. Pleistocene carnivores and humans in eastern Beringia: did short-faced bears really keep people out of North America? In: Gerlach, S.C., Murray, M. (Eds.), Zooarchaeology in the North: People and Animals in Alaska, the Arctic, and northwest North America. British Archaeological Reports 944, pp. 79–101.
- Mathewes, P.E., 2003. Locomotor adaptations and ecomorphology of short-faced bears (*Arctodus simus*) in eastern Beringia, Whitehorse, Yukon Canada. Yukon Palaeontology Program. Department of Tourism and Culture, Yukon.
- Mathewes, P., Burns, J., Weinstock, J., Hofreiter, M., 2004. Pleistocene brown bears in the mid-continent of North America. Science 306, 1150.
- Mathewes, R.W., 1993. Evidence for Younger Dryas-age cooling on the North Pacific coast of America. Quaternary Science Reviews 12, 321–331.
- Mathewes, R.W., Lian, O.B., Clague, J.J., Huntley, M.J.W., 2015. Early Wisconsinan (MIS 4) glaciation on Haida Gwaii, British Columbia, and implications for biological refugia. Canadian Journal of Earth Sciences 52, 939–951.
- Meltzer, D.J., 2009. First Peoples in a New World: Colonizing ice age America. University of California Press, Berkeley 464.
- Meltzer, D.J., 2015. Pleistocene overkill and North American mammalian extinctions. Annual Review of Anthropology 44, 33–53.
- Merriam, C.H., 1889. Description of a new genus *Phenacomys* and four new species of *Arvicoline*. North American Fauna 2, 27–45.
- Merriam, J.C., 1911. Note on a gigantic bear from the Pleistocene of Rancho La Brea. University of California Publications Bulletin of the Department of Geology 6, 163–166.
- Merriam, J.C., Stock, C., 1925. Relationship and structure of the short-faced bear, *Arctotherium*, from the Pleistocene of California. Papers Concerning the Palaeontology of the Pleistocene of California and the Pliocene of Oregon. Carnegie Institution of Washington Contributions to Paleontology 347, 35.
- Miller, C.R., Waits, L.P., Joyce, P., 2006. Phylogeography and mitochondrial diversity of extirpated brown bear (*Ursus arctos*) populations in the contiguous United States and Mexico. Molecular Ecology 15, 4477–4485.
- Meloro, C., 2011. Feeding habits of Plio-Pleistocene large carnivores as revealed by the mandibular geometry. Journal of Vertebrate Paleontology 31, 428–446.
- Mulligan, C.J., Kitchen, A., Miyamoto, M.M., 2008. Updated three-stage model for the peopling of the Americas. PLoS ONE 3, e3199.
- Mustoe, G.E., Harington, C.R., Morlan, R.E., 2005. Cedar Hollow, an early Holocene faunal site from Whidbey Island, Washington. Western North American Naturalist 65, 429–440.
- Nagorsen, D.W., Keddie, G., Hebda, R.J., 1995. Early Holocene black bears, *Ursus americanus*, from Vancouver Island. Canadian Field Naturalist 109, 11–18.
- Nagorsen, D.W., Keddie, G., 2000. Late Pleistocene mountain goats (*Oreamnos americanus*) from Vancouver Island: Biogeographic implications. Journal of Mammalogy 81, 666–675.
- Nixon, G.T., Kelman, M.C., Stevenson, D., Stokes, L.A., Johnston, K.A., 2006. Preliminary Geology of the Nimpkish Map Area (NTS 092L/07), northern Vancouver Island, British Columbia. British Columbia Geological Survey Branch, Geological Fieldwork 2005 135–152 Paper 2006-1.
- Pallas, P.S., 1780. Speciegena zoologica: quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur, Fasciculus, 14, Pauli Berolini, pp. 94.
- Pasitschniak-Arts, M., 1993. *Ursus arctos*. The American society of mammalogists. Mammalian species no. 439, 1–110.
- Pedersen, M.W., Ruter, A., Schweger, C., Fribe, H., Staff, R.A., Kjeldsen, K.K., Marie, M.L.Z., Beaudoin, A.B., Zutter, C., Larsen, N.K., Potter, B.A., Nielsen, R., Rainville, R.A., Orlando, L., Meltzer, D.J., Kjær, K.H., Willerslev, E., 2016. Postglacial viability and colonization in North America's ice-free corridor. Nature 537, 45–49.
- Phipps, C.J., 1774. A voyage towards the North Pole undertaken by His Majesty's command, 1773. Bowyer, W., Nicols, J., for Nourse, London.
- Porter, S.C., Swanson, T.W., 1998. Radiocarbon age constraints on rates of advance and retreat of the Puget Lobe of the Cordilleran ice sheet during the last glaciation. Quaternary Research 50, 205–213.
- Posada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14, 817–818.
- Raghavan, M., Steinrücken, M., Harris, K., Schiffels, S., Rasmussen, S., DeGiorgio, M., et al., 2015. Genomic evidence for the Pleistocene and recent population history of Native Americans. Science 349, 6250.
- Rambaut, A., Drummond, A.J., 2007. Tracer v1.4. <http://beast.bio.ed.ac.uk/Tracer>.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887.
- Richards, R.L., Churcher, C.S., Turnbull, W.D., 1996. Distribution and size variation in North American short-faced bears *Arctodus simus*. In: Stewart, K.M., Seymour, K.L. (Eds.), Palaeoecology and palaeoenvironments of late Cenozoic mammals: tributes to the career of C. S. (Rufus) Churcher. University of Toronto Press, Toronto, pp. 191–246.
- Rohland, N., Hofreiter, M., 2007. Ancient DNA extraction from bones and teeth. Nature Protocols 2, 1756–1762.
- Schubert, B.W., 2010. Late Quaternary chronology and extinction of North American giant short-faced bears (*Arctodus simus*). Quaternary International 217, 188–194.
- Schubert, B.W., Hulbert Jr., R.C., MacFadden, B.J., Searle, M., Searle, S., 2010. Giant short-faced bears (*Arctodus simus*) in Pleistocene Florida USA, a substantial range extension. Journal of Paleontology 84, 79–87.
- Sorkin, B., 2006. Ecomorphology of the giant short-faced bears *Agriotherium* and *Arctodus*. Historical Biology 18, 1–20.
- Steffen, M.L., 2016. Body-size trends in *Peromyscus* (Rodentia: Cricetidae) on Vancouver Island, Canada, with comments on relictual gigantism. Paleobiology 42, 532–546.
- Steffen, M.L., Harington, C.R., 2010. Giant short-faced bear (*Arctodus simus*) from late Wisconsinan deposits at Cowichan Head, Vancouver Island, British Columbia. Canadian Journal of Earth Sciences 47, 1029–1036.
- Stuiver, M., Polach, H.A., 1977. Discussion: reporting of ¹⁴C data. Radiocarbon 19, 355–363.
- Tamm, E., Kivisild, T., Reidla, M., Metspalu, M., Smith, D.G., Mulligan, C.J., Bravi, C.M., Rickards, O., Martinez-Labarga, C., Khusnutdinova, E.K., 2007. Beringian standstill and spread of Native American founders. PLoS ONE 2, e829.
- Valdiosera, C.E., Garcia, N., Anderung, C., Dalen, L., Cregut-Bonnoure, E., Kahlke, R.D., Stiller, M., Brandstrom, M., Thomas, M.G., Arsuaga, J.L., Gotherstrom, A., Barnes, I., 2007. Staying out in the cold: Glacial refugia and mitochondrial DNA phylogeography in ancient European brown bears. Molecular Ecology 16, 5140–5148.
- von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum of Archaeology and Ethnology Bulletin 1. Harvard University, Cambridge 137.
- Voorhies, M.R., Corner, R.G., 1986. The giant bear *Arctodus* as a potential breaker and flaker of late Pleistocene megafaunal remains. Current Research in the Pleistocene 3, 49–51.
- Werner, B.G., Mathewes, R.W., Clague, J.J., 1982. Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of Late Wisconsin Glaciation. Science 218, 675–677.
- Wilson, M.C., Kenady, S.M., Schalk, R.F., 2009. Late Pleistocene *Bison antiquus* from Orcas Island, Washington, and the biogeographic importance of an early postglacial land mammal dispersal corridor from the mainland to Vancouver Island. Quaternary Research 71, 49–61.

- Wilson, D.E., Reeder, D.M. (Eds.), 2005. *Mammal species of the world: a taxonomic and geographic reference*. 3rd edition. Johns Hopkins University Press 2, Baltimore, p. 142.
- Wolverton, S., Lyman, R.L., 1998. Late Quaternary ursid diminution in the Midwest. *Quaternary Research* 49, 322–329.
- Yesner, D.R., 2001. Human dispersal into interior Alaska: antecedent conditions, mode of colonization, and adaptations. *Quaternary Science Reviews* 20, 315–327.
- Zazula, G.D., MacKay, G., Andrews, T.D., Shapiro, B., Letts, B., Brock, F., 2009. A late Pleistocene steppe bison (*Bison priscus*) partial carcass from Tsigehtchic, Northwest Territories, Canada. *Quaternary Science Reviews* 28, 2734–2742.